

NEST DISTRIBUTION OF THE SOLITARY BEE
ANDRENA MACRA MITCHELL (HYMENOPTERA: ANDRENIDAE),
WITH OBSERVATIONS ON NEST STRUCTURE

ERIC W. RIDDICK

Department of Zoology, Howard University, Washington, D.C. 20059. Present address: Division of Biological Control, University of California, 1050 San Pablo Avenue, Albany, California 94706.

Abstract.—The dispersion pattern of nests of the solitary bee *Andrena macra* was estimated, and the nest structure described within nesting sites at Quantico, Virginia. A χ^2 analysis indicated that nests had an aggregated or clumped distribution within each site. A nearest neighbor analysis, however, indicated that the spatial distribution of nests within most dense areas (aggregates) was random. A typical *A. macra* nest contained an entrance, tumulus, main vertical shaft, soil-filled lateral shafts, and 4–12 brood cells.

Key Words: *Andrena*, nest distribution, structure

Andrenid bees are a large group of pollen-gathering insects present on all continents except Australia, with approximately 1200 described species in North America north of Mexico (Hurd 1979). The family is split into the subfamilies Andreninae and Panurginae. In the Nearctic region north of Mexico, the Andreninae contains the genera *Megandrena*, *Ancylandrena*, and *Andrena*. The genus *Andrena* contains 511 described species (Hurd 1979). Most *Andrena* are solitary, which means that each adult female constructs its own nest and mass provisions its brood cells, without any assistance from conspecifics (Michener 1974). Three species are communal, in which females share a common nest but continue to construct and provision their own brood cells. These include *Andrena accepta* Viereck (Rozen 1973), *Andrena crataegi* Robertson (Osgood 1989), and *Andrena erythronii* Robertson (Michener and Rettenmeyer 1956). *Andrena* are typically vernal and univoltine, but *Andrena candida* Smith, *Andrena fulvipennis* Smith, and *Andrena mimetica*

Cockerell have 2 generations in a season (Linsley 1937).

Andrena, as well as many other solitary bees, construct their nests in small to large restricted sites in roadbanks or other open areas. These sites sometimes contain hundreds, even thousands of nests in them (Michener 1974). No prior attempts have been made to determine nest dispersion patterns, for any of the solitary bees nesting in North America. I endeavored to determine whether the nests of the bee *Andrena macra* Mitchell were randomly distributed within several sites, and to describe nest structure. *Andrena macra* is known from West Virginia and Maryland southward to Florida and westward to Texas and Oklahoma (LaBerge 1986). They are vernal, solitary bees that construct their nests in the soil (Sivik 1954, Riddick 1988).

MATERIALS AND METHODS

Nesting sites were found on the United States Marine Corps Reservation at Quantico, Virginia by walking alongside road-

ways and observing bee flight activity, in May 1983. The dimensions of site I were 11×13 m; site II, 40×6 m; site III, 80×5 m; site IV, 20×4 m; and site V, 20×5 m. All sites were on sun-exposed roadsides, had soil of a clay-like consistency, and had sparse amounts of grasses in them. The approximate distance between nesting sites ranged from 1 mile, between sites I and III, to 5 miles, between sites I and IV. The distribution of *A. macra* nests within a site was determined in June and July 1983, at least 2 weeks after *A. macra* females had completed all nesting activities. Nesting site I was investigated from 24–29 June; site II from 6–15 July; site III from 21–27 July; site IV from 1–3 July 1983. Site V was not sampled in 1983. It was assumed that all nest entrances containing tumuli soil mounds represented active nests.

Four sites were artificially subdivided into 1 m^2 sections on graph paper, then a number was assigned to each section going from left to right across a row. Random digits (Rohlf and Sokal 1969) were used to select numbered sections to examine for nest entrances in the real sites. Quadrats (1 m^2) were used to investigate 38–40% of the random sections of sites I, II, and IV. Because of the great size of site III, 40% of the random sections in a 20×5 m portion of it was sampled. The nests found in each quadrat were counted, then observed and expected Poisson frequencies were generated for 5 frequency classes of nests. Frequency classes were 0–4, 5–9, 10–14, 15–19, and 20+ nests. A χ^2 analysis compared the observed and expected Poisson frequencies of nests confined to these classes.

The Coefficient of Dispersion (CD) indicated any deviation from a random distribution of nests within sites. CD represents the variance/mean ratio, which equals 1 in Poisson (random) distributions, is greater than 1 in clumped distributions and less than 1 in regular or even distributions (Sokal and Rohlf 1981).

A nearest neighbor analysis (Clark and

Evans 1954) was used to estimate the spatial distribution of *A. macra* nests at sites III, IV, and V, in May 1985. A m^2 quadrat grid was used to record the precise position (in cm) of each nest entrance along the x, y axes of the quadrat on cm ruled graph paper. The distance to nearest neighbor was measured for each nest from the graph, and the mean observed distance determined. The ratio R equals the observed mean distance/expected mean distance, and measures any departure from random spacing of *A. macra* nests. R equals 1 in a random distribution, but equals 0 in a completely clumped distribution (Clark and Evans 1954). The standard variate of the normal curve, C (Clark and Evans 1954), was used to test the significance of the departure from random spacing of nests. The calculated C values were analogous to critical values in a normal distribution table, at infinite degrees of freedom.

Nest structure was observed at sites II–V on 19 July and 6–16 August in 1984, then 10–11 May and 14–22 June 1985. Approximately 20 excavations were made. A nest entrance that had a tumulus and was at least 20 cm away from any neighboring entrance was selected. The direction and depth of the nest were determined by injecting a mixture of powdered paint and water into the entrance, which then dried and outlined the nest.

RESULTS

Distribution.—*Andrena macra* nests were not randomly distributed in nesting sites. Figure 1 illustrates the observed and expected frequencies for classes of nests per m^2 quadrat. Quadrats containing 0–4 nests were more frequent than expected, those containing 5–9 nests were less frequent than expected and those containing 15 or more nests were more frequent than expected. The χ^2 values greatly exceeded those expected for random distributions (Table 1). A positive deviation from randomness ($\text{CD} > 1.0$) meant that *A. macra* nests were clumped

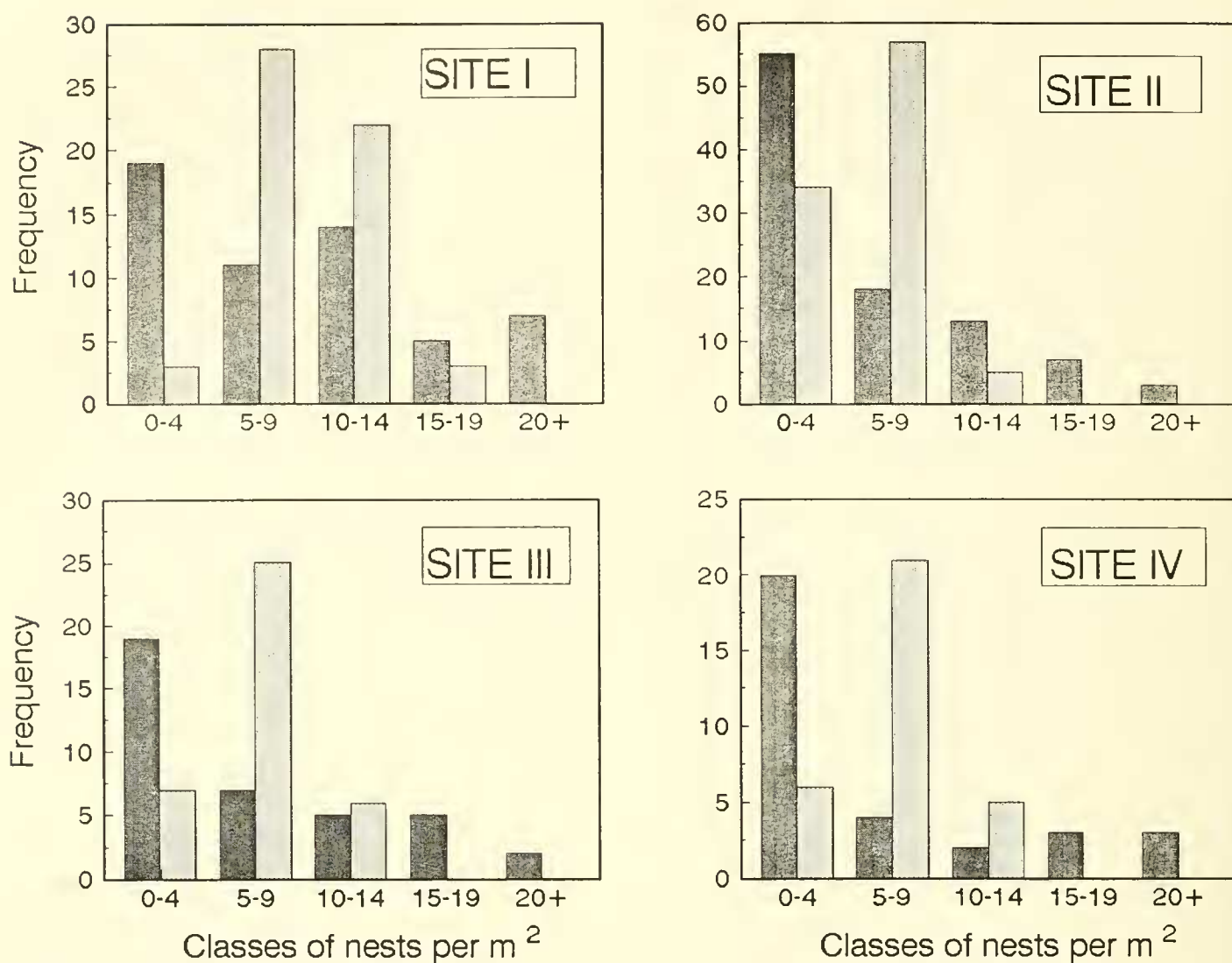


Fig. 1. Frequency diagrams of *A. macra* nest entrances, observed (dark bars) and expected (grey bars), per m² quadrat in nesting sites at Quantico, Virginia.

within nesting sites in 1983. The maximum number of nests found in a m² section ranged from 21, at site III, to 39, at site I. The estimated number of nests in an entire site was 1330 in site I (143 m² area), 1320 in site II (240 m² area), 2800 in site III (400 m² area), and 552 nests in site IV (80 m² area).

Table 2 provides the results of the nearest neighbor analysis for 4 samples, indicating mean distances, observed and expected, between neighboring nests. Distance to neighboring nests ranged from 1–16 cm in sample A, 2–20 cm in sample B, 5–26 cm in sample C, and 2–30 cm in sample D. The R ratio was very close to 1.0 in three of the samples, indicating that spacing between nests was at random within dense areas (aggregates) of sites IV and V, investigated in 1985.

Sample A, however, indicated clumped spacing between nests ($P < 0.05$, site III).

Structure.—A typical *A. macra* nest consisted of an entrance, tumulus, main vertical shaft, one or more lateral shafts, and several brood cells. Nest entrances were positioned on clay textured soil. All entrances had a tumulus, defined as a loose pile of soil pellets removed by the female bee as it constructed its nest. Frequently the tumuli were concentric around the entrances, but on other occasions they were irregular piles on either side of them, on sloped surfaces. The mean nest entrance diameter at site III was 5.8 mm (SEM = 0.08, N = 59 entrances) in a 1 m² area; at site IV, 5.6 mm (SEM = 0.12, N = 17) in a 0.8 m² area, and 6.0 mm (SEM = 0.08, N = 58) in a 0.6 m² area. The mean nest entrance diameter at site V was

Table 1. Mean number of *Andrena macra* nests per m² in nesting sites at Quantico, Virginia in 1983.

Statistic	Nesting Sites			
	I	II	III	IV
Mean number	9.3	5.5	7.0	6.9
SEM	1.1	0.7	1.0	1.6
Sample χ^2	99	53	34	49
df	2	1	1	1
P	<0.001	<0.001	<0.001	<0.001
CD	7.3	7.9	5.6	11.9

5.8 mm (SEM = 0.07, N = 29) in a 1 m² area. Entrances were never blocked with loose soil during nest construction or while the female bee departed the nest to gather pollen-nectar provisions for the brood.

The main nest shaft was a continuation of the entrance and was approximately vertical to the horizontal plane of the roadbank. Shaft inner walls were not coated with any detectable secretion, but they appeared smooth along the entire length. Slight deviations (few cm) away from the vertical plane occurred when pebbles or twigs were avoided, or for no apparent reason. Vertical shaft diameters were approximately the same as entrance diameters along the entire length. Shaft lengths were recorded from complete nests, after the nesting season had ended. The average was 39 cm (SEM = 3.9, N = 8 shafts) at sites II and III combined. Maximum vertical shaft length was 65 cm, minimum was 25 cm. Vertical shafts remained open, or unfilled with loose soil,

after the nests were completed and all brood were deposited.

A lateral shaft is simply a short, angled extension of the main vertical shaft. One back-filled lateral shaft was disclosed in a completed nest, and was found to angle at 30–40° downward, from the end of the vertical shaft. It began at 36 cm and was traced to a depth of 42 cm. Unfortunately, it did not clearly end at a brood cell, but cells were situated around it and 2–3 cm beneath it. A non-filled lateral shaft of a nest in an early stage of completion began at the end of the main vertical shaft (37 cm beneath the surface), and ended with an unprovisioned brood cell, 41 cm below the surface. A provisioned and sealed brood cell was 2 cm below the first. The lateral shaft leading to the second cell was not detected.

Brood cells were urn-shaped and composed of two walls, an outer wall of compacted soil and an inner wall of a thin shiny, waxy lining. Each slanted upwards, with the

Table 2. Nearest neighbor analysis of *A. macra* nests in dense areas of sites III, IV, and V at Quantico, Virginia in 1985.

Statistic	Samples			
	A	B	C	D
N (measurements)	59	58	17	29
Area (m ²)	1.0	0.6	0.8	1.0
Obs. mean distance (cm)	5.52	5.17	11.35	9.17
SEM	0.484	0.476	1.74	1.25
Exp. mean distance (cm)	6.51	5.08	10.85	9.28
R	0.848	1.02	1.046	0.988
P	<0.05	>0.5	>0.5	>0.9
Site	III	IV	IV	V

cell cap directed toward the surface at a 30–40° angle, from the vertical axis. Mean inner brood cell dimensions were 6.2×10.5 mm ($N = 5$ cells). The mean number of brood cells contained in a completed nest was 8.3 ($SEM = 0.7$, $N = 9$ nests), at sites II and III combined, with a maximum of 12 and a minimum of 4 per nest. Mean brood cell depth beneath the surface of site II was 44.4 cm ($SEM = 1.8$, $N = 22$ cells), with a maximum depth of 57 cm and minimum of 30 cm. The mean cell depth beneath site III was 59.8 cm ($SEM = 3.3$, $N = 6$ cells), with a maximum of 68 cm and minimum of 46 cm. Cells were positioned several cm beneath the end of the main vertical shaft, and all were clustered within a 5 cm radius of this shaft. Lateral shafts leading to the cells were not disclosed.

DISCUSSION

Distribution.—Hundreds of *A. macra* nests were found in well defined sites on sloping roadside shoulders in soil of mostly clay texture and sparse grass. Large nesting sites may benefit the offspring by increasing the opportunities for mating, as they emerge in early May. Mating occurred on the surface, where males were often seen pouncing on females, as they approached the entrances to their nests (Riddick 1988). Other *Andrena* are known to mate at nesting sites and at floral resources (Barrows 1978).

Large nesting sites have been reported previously for many species of solitary, soil nesting bees (Michener 1974), but the reasons why they persist in restricted areas remain equivocal (Michener et al. 1958, Cane 1991). Butler (1965) suggested that site odor restricts nest building to specific areas even when other suitable areas are close at hand. He transplanted a portion of an *Andrena flavipes* Panzer nesting site, while these bees were overwintering in brood cells, into an unused gravel pit. The following spring season, males and females emerged and many remained in the area around the pit. Mating was observed and female *A. flavipes* con-

structed new nests in this pit. This newly established site persisted for 5 years (Butler 1965). The chemical secretions released from the female bee's Dufour's gland are used in nest construction and nest marking (Hefetz 1987), but may also be the source of olfactory cues that induce males and females to remain at the nesting site (Duffield et al. 1984). The smell of emerging females or freshly excavated tumulus soil may attract other emerging *A. macra* to remain at the natal site then begin constructing their own nests, or maybe reusing natal nests. Nest reuse has been reported for *Andrena dunningi* Cockerell (Johnson 1981) and *Andrena viburnella* Graenicher (Stephen 1966). Philopatry, or the tendency of offspring to remain at the nesting site from which they were reared, is a possible means by which nest aggregations are initiated (Rosenheim 1990).

It is interesting to note that *A. macra* nests were not randomly distributed in the sites (Table 1), since many were found in a small proportion of the examined m^2 quadrats. The nest dispersion pattern found for this species may be common to all *Andrena*, but no comparable studies have been reported. However, the densities of nests in sample areas of nesting sites are reported for other species. For example, *Andrena alleghaniensis* Viereck nest density was as much as 43/ m^2 (Batra 1990), *Andrena candida* Smith ranged from 1 to 5 nests/ m^2 (Youssef and Bohart 1968), *Andrena erigeniae* Robertson ranged from 1 to 21 nests/ m^2 (Davis and LaBerge 1975), and *Andrena viburnella* Graenicher ranged from 10 to 380 nests/ m^2 . Sivik (1954) reported 4.6 nests/ yd^2 for an *A. macra* nesting site in North Carolina. The mean number of nests/ m^2 quadrat ranged from 5.5 to 9.3 (Table 1) for *A. macra* nesting in Virginia, suggesting a moderate nest density, when compared to other species.

Andrena macra nesting sites persist for years. A site near Raleigh, North Carolina persisted for at least 19 years (Sivik 1954).

The sites in Quantico, Virginia were first discovered in May 1983 and were still active in May 1987, as females were observed entering nest entrances laden with pollen.

Structure.—The mean nest entrance diameter for *A. macra* nests ranged from 5.6–6.0 mm. Entrance diameters for other species range from 3.6 mm for *A. candida* nests (Youssef and Bohart 1968) to 7.5–9.0 mm for *Andrena carlini* Cockerell and *Andrena regularis* Malloch nests (Schrader and LaBerge 1978). Diameters are directly correlated with bee size; the larger the female bee, the larger its entrance diameter.

Andrena macra nest entrances were surrounded by tumuli. Each was composed of soil pellets removed during nest construction. Several species build their nests in sandy soil and, as a consequence, lack tumuli because of wind erosion. These include western species, *A. accepta* (Rozen 1973) and *Andrena placida* Smith (Thorp and Stage 1968), and an eastern species, *A. alleghaniensis* (Batra 1990). *Andrena macra* did not intentionally plug nest entrances with loose soil. However, some entrances were temporarily blocked while the females were excavating soil late in the day. *Andrena regularis* (Schrader and LaBerge 1978) and *A. viburnella* (Stephen 1966) nest entrances were similarly blocked with soil during excavations. *Andrena haynesi* Viereck and Cockerell plug their nest entrances with moist sand when not foraging (Parker and Griswold 1982).

One vertical shaft per nest is typical for *A. macra* and most other solitary *Andrena*. It is not filled with loose soil after nest completion. Species that back-fill their nest vertical shaft include *A. candida* (Youssef and Bohart 1968), *A. erythronii* (Michener and Rettenmeyer 1956), *A. regularis* (Schrader and LaBerge 1978), and *A. viburnella* (Stephen 1966).

Nest lateral shafts were back-filled with loose soil by *A. macra*, after nest completion. Many *Andrena* do the same. Some examples include: *A. accepta* (Rozen 1973), *A.*

alleghaniensis (Batra 1990), *A. candida* (Youssef and Bohart 1968), *A. chalybaea* (Cresson) (Thorp 1969), *A. erigeniae* (Davis and LaBerge 1975), *A. erythrogaster* Ashmead (Miliczky 1988), *A. erythronii* (Michener and Rettenmeyer 1956), *A. foxii* Cockerell (Linsley et al. 1973), *A. helianthi* Robertson (Parker and Bohart 1982), *A. oenotherae* Timberlake (Linsley and MacSwain 1956), and *A. viburnella* (Stephen 1966). Back-filling lateral shafts is a means of protecting the brood from predators and parasites.

Andrena macra brood cells were urn-shaped, composed of an outer wall of compacted soil, and an inner wall or lining made from a wax-like substance. This cell shape and wall composition is typical for other *Andrena* nests. Inner linings are secreted from the female's Dufour's gland (Cane 1981). This secretion waterproofs the cell (Thorp 1969), maintains cell humidity and deters microbial growth (Duffield et al. 1984). Brood cell depth ranged from 30–68 cm beneath the surface at *A. macra* nesting sites II and III. Other *Andrena* nest cell depths range from 3–8 cm for *A. dunningi* (Johnson 1981), 15–60 cm for *A. placida* (Thorp and Stage 1968), to 270 cm for *A. haynesi* nesting on sand dunes in Utah (Parker and Griswold 1982). *Andrena* may position their brood cells at a certain depth, depending on the soil moisture content at the nesting site. This suggests that cell depth will vary from one locality to the next.

The average number of brood cells per nest was 8 (range 4–12), for *A. macra*. *Andrena alleghaniensis* nests contain 1–2 cells (Batra 1990), *A. candida* nests have 2–4 cells (Youssef and Bohart 1968), while each *A. viburnella* nest has 12–14 cells (Stephen 1966). The number of cells produced by each female *Andrena* may depend on the availability of floral resources.

Summary.—*Andrena macra* nests displayed a clumped dispersion pattern within 4 sites in Virginia. However, nests were randomly spaced from neighboring ones within

3 of 4 dense areas (aggregates) sampled. An *A. macra* nest contained a single entrance-exit opening, tumulus, single main vertical shaft, soil-filled lateral shafts, and an average of 8 brood cells. Cell number per nest and maximum cell depth beneath the surface were greater for *A. macra* nests than for the nests of many solitary species in North America. *Andrena* are pollinators of many wildflowers, agricultural crops and trees (Batra 1990, Miliczky et al. 1990). Transplanting portions of nesting sites, with the brood intact, into fruit tree orchards is a potential way of encouraging pollination by these indigenous bees. *Andrena* are efficient pollinators of apple in Ontario (Boyle-Makowski 1987).

ACKNOWLEDGMENTS

Dr. Wallace E. LaBerge, at the Illinois Natural History Survey, identified the bees. Ms. Alexis T. Tolbert assisted with counting nest entrances. I thank Dr. Richard Duffield and Dr. George Middendorf for their encouragement during this investigation. This research was part of a Master's thesis submitted to the graduate faculty, Department of Zoology, at Howard University.

LITERATURE CITED

- Barrows, E. M. 1978. Male behavior in *Andrena erigeniae* (Hymenoptera: Andrenidae) with comparative notes. *Journal of the Kansas Entomological Society* 51: 798-806.
- Batra, S. W. T. 1990. Bionomics of a vernal solitary bee *Andrena (Scapteropsis) alleghaniensis* Viebeck in the Adirondacks of New York (Hymenoptera: Andrenidae). *Journal of the Kansas Entomological Society* 63: 260-266.
- Boyle-Makowski, R. M. D. 1987. The importance of native pollinators in cultivated orchards: Their abundance and activities in relation to weather conditions. *Proceedings of the Entomological Society of Ontario* 118: 125-141.
- Butler, C. G. 1965. Sex attraction of *Andrena flavipes* Panzer (Hymenoptera: Andrenidae) with some observations on nest site restriction. *Proceedings of the Royal Entomological Society of London (A)* 40(4-6): 77-80.
- Cane, J. H. 1981. Dufour's gland secretion in the cell linings of bees (Hymenoptera: Apoidea). *Journal of Chemical Ecology* 7: 403-410.
- . 1991. Soils of ground-nesting bees (Hymenoptera: Apoidea): Texture, moisture, cell depth and climate. *Journal of the Kansas Entomological Society* 64: 406-413.
- Clark, P. J. and F. C. Evans. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. *Ecology* 35: 445-453.
- Davis, L. R., Jr. and W. E. LaBerge. 1975. The nesting biology of the bee *Andrena (Ptilandrena) erigeniae* Robertson (Hymenoptera: Andrenidae). Illinois Natural History Survey, Biological Notes 95. 16 pp.
- Duffield, R. M., J. W. Wheeler, and G. C. Eickwort. 1984. Sociochemicals of bees, pp. 387-428. In Bell, W. J., and R. T. Carde, eds., *Chemical Ecology of Insects*. Chapman and Hall, London.
- Hefetz, A. 1987. The role of Dufour's gland secretions in bees. *Physiological Entomology* 12: 243-253.
- Hurd, P. D., Jr. 1979. The Apoidea, pp. 1741-2209. In Krombein, K. V., D. R. Smith, and B. D. Burks, eds., *Catalog of Hymenoptera in America North of Mexico*. Vol 2. Smithsonian Institution Press, Washington, D.C.
- Johnson, M. D. 1981. Observations on the biology of *Andrena (Melandrena) dunningi* Cockerell (Hymenoptera: Andrenidae). *Journal of the Kansas Entomological Society* 54: 32-40.
- LaBerge, W. E. 1986. A revision of the bees of the genus *Andrena* of the Western Hemisphere. Pt. XII. Subgenera *Leucandrena*, *Ptilandrena*, *Scoliadrena*, and *Melandrena*. *Transactions of the American Entomological Society* 112: 191-248.
- Linsley, E. G. 1937. The occurrence of double broods in North American andrenid bees (Hymenoptera). *Bulletin of the Brooklyn Entomological Society* 32: 125-127.
- Linsley, E. G. and J. W. MacSwain. 1956. Further notes on the taxonomy and biology of the andrenine bees associated with *Oenothera* (Hymenoptera: Andrenidae). *Pan-Pacific Entomologist* 32: 111-121.
- Linsley, E. G., J. W. MacSwain, P. H. Raven, and R. W. Thorp. 1973. Comparative behavior of bees and Onagraceae. V. University of California Publications in Entomology 71: 1-68.
- Michener, C. D. 1974. The Social Behavior of the Bees. A Comparative Study. Belknap Press of Harvard University Press, Cambridge. 404 pp.
- Michener, C. D. and C. W. Rettenmeyer. 1956. The ethology of *Andrena erythronii* with comparative data on other species (Hymenoptera: Andrenidae). *University of Kansas Science Bulletin* 37: 645-684.
- Michener, C. D., R. B. Lange, J. J. Bigarella, and R. Salamuni. 1958. Factors influencing the distribution of bees' nests in earth banks. *Ecology* 39: 207-217.

- Miliczky, E. R. 1988. Observations on the bionomics of the bee *Andrena* (*Tylandrena*) *erythrogaster* Ashmead (Hymenoptera: Andrenidae). Illinois Natural History Survey, Biological Notes 130. 18 pp.
- Miliczky, E. R., D. F. Mayer, and J. D. Lunden. 1990. Notes on the nesting biology of *Andrena* (*Melandrena*) *nivalis* Smith (Hymenoptera: Andrenidae). Journal of the Kansas Entomological Society 63: 166–174.
- Osgood, E. A. 1989. Biology of *Andrena crataegi* Robertson (Hymenoptera: Andrenidae), a communally nesting bee. Journal of the New York Entomological Society 97: 56–64.
- Parker, F. D. and G. E. Bohart. 1982. Notes on the biology of *Andrena* (*Callandrena*) *helianthi* Robertson (Hymenoptera: Andrenidae). Pan-Pacific Entomologist 58: 111–116.
- Parker, F. D. and T. Griswold. 1982. Biological notes on *Andrena* (*Callandrena*) *haynesi* Viereck and Cockerell (Hymenoptera: Andrenidae). Pan-Pacific Entomologist 58: 284–287.
- Riddick, E. W. 1988. The nesting biology of the bee *Andrena macra* with observations and rearing of its parasites. Unpublished Master's thesis. Howard University, Washington, D.C. 127 pp.
- Rohlf, F. J. and R. R. Sokal. 1969. Statistical Tables. W. H. Freeman and Company, San Francisco. 253 pp.
- Rosenheim, J. A. 1990. Density-dependent parasitism and the evolution of aggregated nesting in solitary Hymenoptera. Annals of the Entomological Society of America 83: 277–285.
- Rozen, J. G., Jr. 1973. Biology notes on the bee *Andrena accepta* Viereck (Hymenoptera: Andrenidae). Journal of the New York Entomological Society 81: 54–61.
- Schrader, M. N. and W. E. LaBerge. 1978. The nesting biology of the bees *Andrena* (*Melandrena*) *regularis* Malloch and *Andrena* (*Melandrena*) *carlini* Cockerell (Hymenoptera: Andrenidae). Illinois Natural History Survey, Biological Notes 108. 24 pp.
- Sivik, F. P. 1954. Ecological notes on three species of solitary bees. Entomological News 65: 253–256.
- Sokal, R. R. and F. J. Rohlf. 1981. Biometry. W. H. Freeman and Company, New York. 859 pp.
- Stephen, W. P. 1966. *Andrena* (*Cryptandrena*) *vi-burnella*. I. Bionomics. Journal of the Kansas Entomological Society 39: 42–51.
- Thorp, R. W. 1969. Systematics and ecology of bees of the subgenus *Diandrena* (Hymenoptera: Andrenidae). University of California Publications in Entomology 52: 1–146.
- Thorp, R. W. and G. I. Stage. 1968. Ecology of *Andrena placida* with descriptions of the larva and pupa. Annals of the Entomological Society of America 61: 1580–1586.
- Youssef, N. N. and G. E. Bohart. 1968. The nesting habits and immature stages of *Andrena* (*Thysandrena*) *candida* Smith. Journal of the Kansas Entomological Society 41: 442–455.